1   # On a wing and a prayer: limitations and gaps in global bat wing
2   # morphology trait data
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9   ## Abstract

10   Species' life history traits have a wide variety of applications in ecological and conservation

11   research, particularly when assessing threats. The development and growth of global species trait

12   databases are critical for improving trait-based analyses; however, it is vital to understand the gaps

13   and biases of available data. Bats are an extremely diverse and widely distributed mammalian

14   order, with many species facing local declines and extinction. We conducted a literature review

15   for bat wing morphology, specifically wing loading and aspect ratio, to identify issues with data

16   reporting and ambiguity. We collected data on field methodology, trait terminology, and data

17   reporting and quality. We found several issues regarding semantic ambiguity in trait definitions

18   and data reporting. Globally we found that bat wing morphology trait coverage was low. Only six

19   bat families had over 40% trait coverage, and of those none consisted of more than 11 total species.

20   We found similar biases in trait coverage across IUCN Redlist categories with threatened species

21   having lower coverage. Geographically, North America, Europe, and the Indomalayan regions

22   showed higher overall trait coverage, while both the Afrotropical and Neotropical ecoregions

23   showed poor trait coverage. The underlying biases and gaps with bat wing morphology data have

24   implications for researchers conducting global trait-based assessments. Implementing imputation

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25   techniques may address missing data, but only for smaller regional subsets with substantial trait

26   coverage. However, due to the low overall trait coverage, increasing species representation in the

27   database should be prioritized. We suggest adopting an Ecological Trait Standard vocabulary to

28   reduce semantic ambiguity in bat wing morphology traits to improve data compilation and clarity.

29   Additionally, we advocate that researchers adopt an Open Science approach to facilitate the growth

30   of a bat wing morphology trait database.

31   **Keywords**: Chiroptera, species traits, wing loading, aspect ratio, spatial biases, taxonomic biases,

32   open science, reproducibility

1. Introduction

34   Bats are an incredibly diverse group constituting nearly one-fifth of all mammals and the second

35   most diverse group of mammals globally. Bats provide a wide range of ecosystem services such

36   as seed dispersal (Melo et al., 2009; Seltzer, Ndangalasi & Cordeiro, 2013) and pest control (Kunz

37   et al, 2011; Maas et al, 2016). Globally, bat populations are under threat from a wide range of

38   pressures (O'Shea et al., 2016; Frick, Kingston & Flanders, 2020) such as habitat loss and

39   degradation (Meyer et al., 2016), wind farms (Arnett el al, 2016), and hunting (Mickleburgh,

40   Waylen & Racey, 2009). Despite their ecological importance and conservation threats, bats have

41   a notable lack of information when compared to other mammals and birds (Frick, Kingston &

42   Flanders, 2020).

43   Species traits, here defined as measurable characteristics of an organism, provide a wide range of

44   applications for understanding systematics and macroevolution (Harmon et al., 2010; Zamudio,

45   Bell & Mason, 2016) as well as species conservation (Jones, Purvis & Gittleman, 2003; Pacifici et

46   al., 2015). Traits provide an important link to the functional role of species within an ecosystem,

47   and as such trait-based models for vulnerability are a valuable tool (Pacifici et al., 2015; Ramirez-

48   Bautista et al., 2020). However, the ability to apply trait-based assessments relies on having the

49   appropriate trait coverage. Hortal et al (2015) presented the concept of the Raunkiaeran shortfall

50   to describe the lack of knowledge on ecologically relevant species traits, as an important factor to

51   consider when applying large-scale ecological analyses. Biases in the underlying trait data

52   availability can lead to subsequent biases in any analyses. Typically, vertebrate trait data

53   availability is biased taxonomically towards large more widely distributed species and with less

54   representation for reptiles and amphibians, and geographically with less representation in

55   biologically diverse tropical regions (González-Suárez, Lucas & Revilla, 2012; Etard, Morrill &

56   Newbold, 2020). Understanding the underlying biases in a species trait or collection of traits is

57   critical in assessing their applicability to any analysis.

58   Wing morphology is an important trait in bats, as it links many different natural history traits such

59   as diet (Norberg & Rayner, 1987; Norberg & Fenton, 1988), habitat association (Brigham, Francis

60   & Hamdorf, 1997; Jennings et al., 2004), and range size (Luo et al., 2019). Bat wing morphology

61   is traditionally described using aspect ratio and wing loading (Norberg & Rayner, 1987). For bats

62   wing morphology, aspect ratio is typically defined as the wingspan squared divided by wing area,

63   which describes flight efficiency and maneuverability (Norberg & Rayner, 1987). Higher aspect

64   ratios (e.g. short, wide wings), correspond with faster turning but less efficient flight compared

65   with higher aspect ratios (e.g. long, narrow wings) seen in more efficient flight such as soaring

66   (Norberg & Rayner, 1987; Norberg, Brooke & Trewhella, 2000). Wing loading is calculated by

67   dividing the weight (mass * gravity) of the bat by the wing area and provides a measure of lift

68   potential and influences maneuverability and flight speed. In addition to identifying natural history

69   traits, bat wing morphology has been used for conservation to predict extinct risk (Jones, Purvis &

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70   Gittleman, 2003), habitat fragmentation vulnerability (Farneda et al, 2015), and association with

71   urbanization (Jung and Threlfall, 2018). Thus, wing morphology is likely a useful metric for any

72   trait-based assessment with bats.

73   Globally available databases for species traits are proliferating, as they provide an open repository

74   for assessment (Jones et al., 2009; Kattge et al, 2011; Oliveira et al., 2017). Norberg and Raynor

75   (1987), compiled a global wing morphology database for bats and since then other studies have

76   attempted to compile bat wing morphology either for specific regions (Marinello & Bernard, 2014)

77   or globally (Jones, Purvis & Gittleman, 2003); however, a single centralized and open database

78   does not currently exist for bat wing morphology. Prior to compiling a unified trait database,

79   several key factors must be considered. First, compiled data should use standardized measurement

80   and recording protocols among studies, including following a well-defined and standardized

81   vocabulary (Schneider et al., 2019; Gallagher et al, 2020). Additionally, global trait databases

82   typically contain large volumes of missing data. Missing data can occur both randomly and non-

83   randomly (e.g. geographically, taxonomically) creating potential biases that need to be understood

84   to appropriately validate any results when using a data set, however, missing data can also be

85   imputed to generate larger usable data sets (Taugourdeau et al., 2014).

86   Our paper seeks to analyze issues associated with developing a global bat wing morphology

87   database. Through a comprehensive literature review, we identify reporting and methodological

88   issues for comparability. Understanding the underlying biases in global trait data is essential in

89   assessing that ability to apply it to global analyses as well as highlight important regions or species

90   to prioritize for study. We created a synthesized dataset for bat wing morphological traits, and then

91   assessed underlying biases in species data availability.

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92 2. Methodology

93 2.1 Literature review

94 In September 2019 and again in February 2020 we searched Scopus and Web of Science databases

95 for articles relating to bat wing morphology, Additionally, we searched Google Scholar using

96 Publish or Perish (Harzing, 2007) software keeping only the first 300 results (Haddaway et al.,

97 2015). For each database we used the following terms: "wing" AND ("morphology" OR "shape"

98 OR "loading" or "measurements") AND ("bat*" or "chiroptera"). Finally, we also included studies

99 found through reference lists in papers identified from the systematic searches.

100 To screen papers, we adopted the PRISMA reporting procedure outlined in by Moher, Telzlaff,

101 and Altman (2009). We excluded any papers that did not 1) study bat wing morphology (e.g. birds

102 or robotics), 2) use wing morphology in their study (e.g. only reference wing morphology in the

103 Discussion) or 3) collect primary wing morphology (e.g. reviews and meta-analysis).

104 From each paper included in the analysis, we collected data on the basic methodology including

105 whether the study used live bats or specimens, the wing area measurement method (e.g. photo,

106 tracing), and whether they used only primary data. Norberg & Raynor (1987) noted important

107 semantic ambiguity in the term "wing area", and whether the body and/or tail membrane is

108 included. We followed Bininda-Emonds & Russell, 1994 and use two distinct terms lifting surface

109 area (LSA) and wing area (WA). Lifting surface area is defined following "wing area" set out by

110 Norberg & Raynor (1987) which includes the area of the tail membrane, body excluding the head,

111 and wing. We define wing area specifically referring to the area of the patagium only. To assess

112 methods reporting quality we recorded whether the paper explicitly reported whether they used

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113   LSA or WA. When the paper was unclear, we attempted to extrapolate which definition was used

114   based on provided figures or references.

115   We also collected information on data reporting and whether the study provided data for both

116   direct field measures, mass, forearm, wingspan, and wing area as well as calculated variables,

117   aspect ratio, wing loading, and relative wing loading. We considered data that were only displayed

118   in a figure as absent because raw values could not be extracted. Recent work supports importance

119   of incorporating and providing intraspecific trait variability (Guralnick et al., 2016; Kissling et al.,

120   2018), thus we also evaluated the reported data quality based on whether the study provided raw

121   data for individuals, means and standard deviations, or only as means without SDs or sample sizes.

2.2 Data availability and biases

123   We assessed global data availability for bat wing morphology to assess taxonomic and geographic

124   trends. First, we validated and updated the species names from the literature as older papers often

125   used outdated scientific names; however, as different taxonomic backbones exist, we retained the

126   original verbatim scientific name provided. As we investigated patterns in conservation status

127   based on the IUCN Redlist, we corrected our scientific names to match the IUCN convention. We

128   first checked for synonyms in the GBIF backbone naming system, and then followed the IUCN

129   naming convention to allow for extracting threat status. We downloaded data on geographic realm

130   and IUCN Redlist Conservation Status for each species, using package "rredlist" (Chamberlain,

131   2020). We did not include data when individuals were not identified to species in the study, nor

132   species that did not occur on the IUCN species list nor the Catalogue of Life. For valid species that

133   did not occur on the IUCN Redlist we manually added the conservation status (Data Deficient)

134   and realm (following the IUCN convention). We followed the terminology presented in Etard et

135   al. (2020) for assessing trait data availability, with trait coverage referring to the proportion of

136   missing data for a specific trait, and trait completeness which is the proportion of traits have an

137   available estimate for a given species. We then evaluated trait coverage and completeness based

138   on conservation status, taxonomic family, and realm to review patterns.

139   We assessed spatial patterns in trait coverage by first descriptively comparing the overall trait

140   coverage for the ecoregions Palearctic, Nearctic, Neotropical, Afrotropical, Indomalayan, and

141   Australasian ecoregions (following the WWF Ecoregions classification; Olson et al., 2004). Since

142   the Palearctic realm covers a large geographic area, we further divided the area by geopolitical

143   divisions into Asiatic Palearctic (Asiatic Russia and Eastern Asian), European Palearctic, Middle

144   Eastern Palearctic (consisting of Central and Southwestern Asia), and Palearctic Africa.

145   Additionally, we reviewed the assemblage-level trait coverage for wing loading and aspect ratio

146   for each ecoregion. We overlapped species distributions from IUCN (Spatial Range Dataset IUCN,

147   2020; downloaded October, 2020) and calculated the assemblage-level trait coverage globally

148   using a grid size of approximately 50 km by 50 km using the package "fasterize" in R (Ross,

149   2020). We then extracted the median and interquartile range for trait coverage values in each

150   ecoregion.

2.3 Trait data extraction, validation, and compilation

152   When available, we extracted morphological data to compile a unified data set. As our objective

153   was to compile a generalized database on bat species wing morphology, we first combined data

154   for species within studies (e.g. when studies reported values for different sexes). For studies that

155   used wing area instead of LSA we used the correction based on taxonomic family used by Norberg

156   and Raynor (1987) which added the tail and body area as a percentage of reported wing area (20%

157   Emballonurids, Rhinolophids, Hipposiderids, and Mormoopids, 25% for Verpertilionids, and 16%

158   for Phyllostomidids).

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159   When wing loading and/or relative wing loading was not reported but mass and wing area were,

160   we estimated a mean wing loading and considered the estimate as a single observation, and thus

161   did not calculate standard deviation. We also applied this procedure to estimate aspect ratio and

162   relative wing loading. We estimated wing loading from relative wing loading and vice versa when

163   only mass and either wing loading or relative wing loading were reported.

164   We created a compiled data set with wing morphology data based on the reviewed literature. Prior

165   to combining estimates for species from different studies we identified outlier records and either

166   corrected or removed the data. To identify outliers, we first calculated the mean standard deviations

167   for aspect ratio and wing loading. We defined an outlier as any species that exhibit a standard

168   deviation above 1.5 times the mean. For the species we identified we reviewed all data from studies

169   reporting for those species to determine whether the study exhibited systematic biases. For studies

170   that exhibiting systematic biases we sought to identify and then rectify the issue, and if we could

171   not then the data from the study was excluded from the final global data set. For individual species

172   outliers (e.g. when the study did not exhibit systematic biases) we removed records that did not

173   report sample size and standard deviation. We did not remove outliers, if the variation in the data

174   arose potentially due to geographic or taxonomic variation (e.g. different sub-species).

175   Additionally, when forearm and/or were missing for a species, we used values from the

176   PanTHERIA database (Jones et al., 2009) when available. We used the finalized data set to

177   evaluate patterns in missing data taxonomically, geographically, and in conservation status.

178   2.4 Methodological impact assessment

179   We investigated the effect of area measurement method and area definition on wing area/lift

180   surface area values. From our methodological review, we only included studies that clearly

181   reported how wing area was defined and how wing area was measured. Next, we only included

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182   species that had area measurements from at least two different methods and specifically stated in

183   the methods that they used the lifting surface area definition for "wing area". The available data

184   did not provide a large enough sample to make viable comparisons between wing area definitions

185   for different families (only 5 species from 3 genera had measurements for both definitions). We

186   ran Bayesian generalized linear mixed model using the package "*brms*" in R Studio (Bürkner,

187   2017), with a lognormal likelihood, and 6 chains with 6,000 iterations each (1,000 set as burn-in).

188   We kept default flat priors, with measurement method (tracing vs. photograph) set as a fix8282.ed

189   effect, and species and study ID as random effects. We checked for model convergence using trace

190   plots and R-hat values, and assessed model fit through posterior predictive checks, leave-one-out

191   cross-validation and Bayesian R^2 (Bürkner, 2017). We ran all analyses and visualizations in R

192   Studio using R v3.6.3 (R Core Team, 2020)

3. Results

3.1 Method variation and reproducible reporting

195   Our search returned 738 references and yielded 147 sources after screening and full-text

196   assessment (Supp File S1) covering 508 species from 18 families. Area measurement techniques

197   varied, but most studies either used wing tracings (n = 71) or photographs (n = 49), with ~10% of

198   studies not reporting how area measurements were obtained (n = 15; Figure 1). Other methods

199   included using photos of bats in flight, or directly estimating area in the field with a planimeter.

200   Roughly half of the studies reviewed clearly distinguished whether they used LSA or wing area

201   (56.4%), while 24.8% did not report methods in a way that an area definition could be extrapolated

202   (Figure 1). All but three studies used the term "wing area", regardless of the area definition

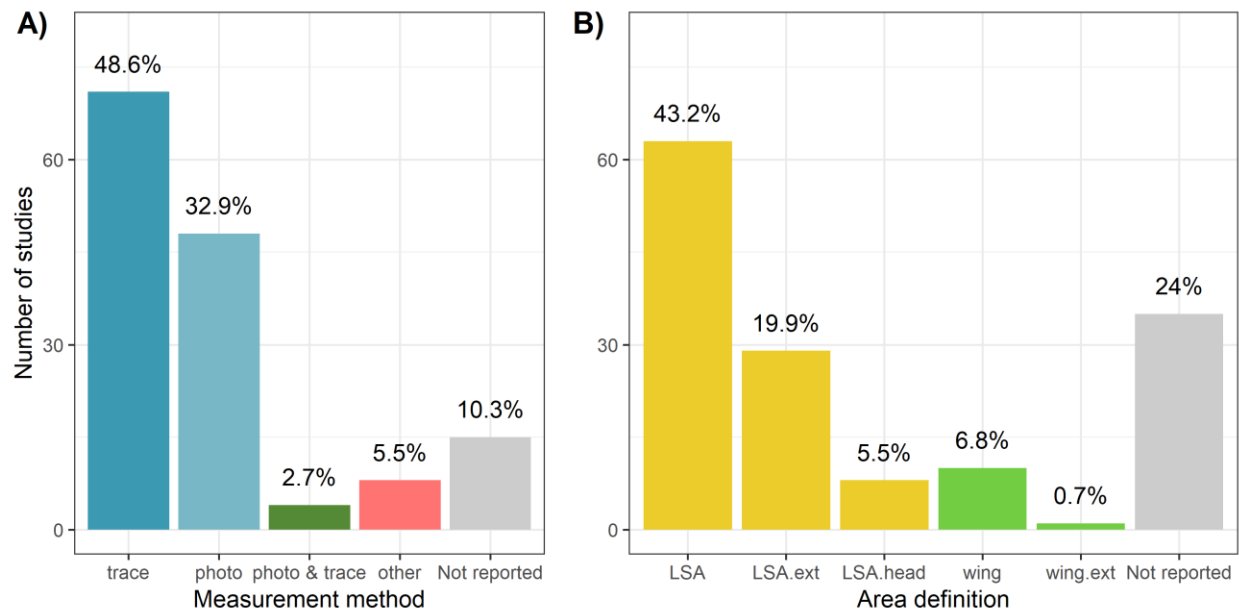203   described in the methodology.

Figure 1 Methods used to measure wing area in bats (A), and how studies defined wing area either using lift surface area (LSA) or wing area (wing) with "ext" denoting that the definition was extrapolated based on the provided reference. Lift surface area includes the area of the patagium uropatagium, and the body excluding the head, and wing area refers to only the area of the patagium.

Overall, 83 studies (56.5 %) provided all the relevant trait measurements (mass, wingspan, wing area) for calculating wing loading, relative wing loading, and aspect ratio. Conversely, 19 studies did not report data for directly measured traits, and a further five studies did not report any raw data despite using the data for analysis. For directly measured traits, both wingspan and wing area exhibited higher missing data rates than mass (Figure 2).
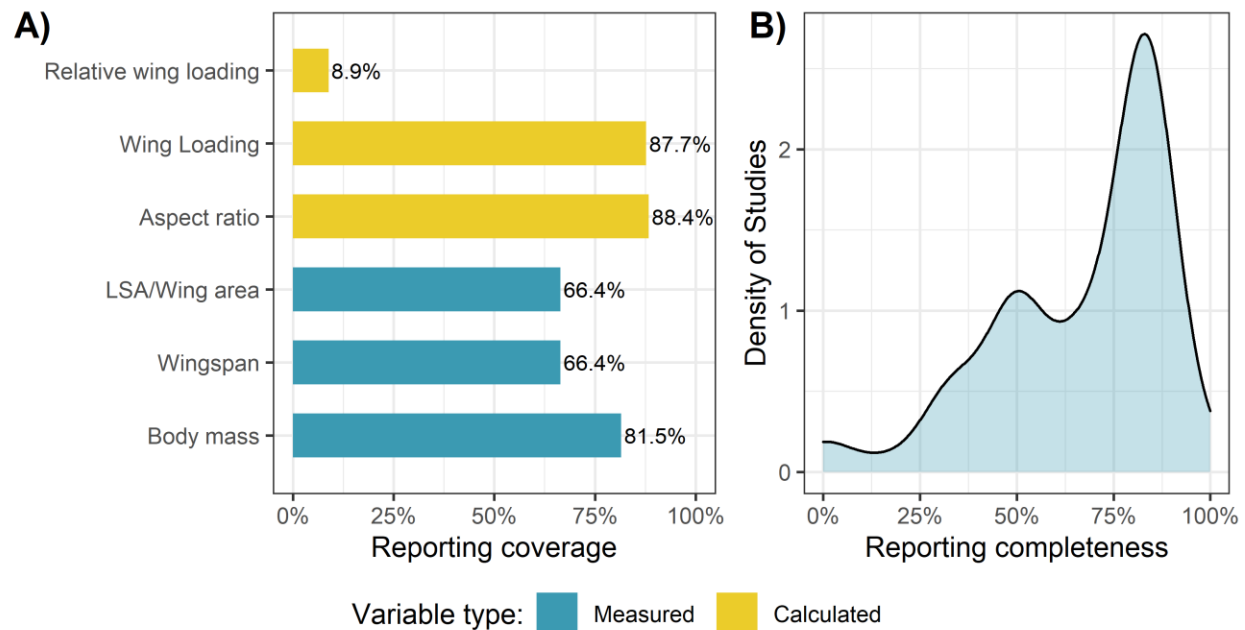
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Figure 2 A) Reporting coverage for each bat wing morphology trait and the B) density of reporting completeness for studies that collected bat wing morphology traits.

Measured traits had a higher missing rate than calculated variables, except for relative wing loading, which was not typically calculated (only 15 of 147 studies calculated RWL with 13 reporting values). Of the 13 studies that reported relative wing loading, two studies did not provide the base measurements mass and/or wing area to estimate wing loading. However, the data loss of those two studies resulted in 66 records and 14 unique species not having available wing loading data. Similarly, 19 studies that did not report relative wing loading also did not provide the necessary data to calculate relative wing loading, leading to 24 unique species without relative wing loading estimates. Not reporting mass led to a loss of 38 species with complete wing morphology data from the final database. From the literature we identified 487 species which had estimates for both wing loading and aspect ratio. Overall, reporting issues and methodological inconsistencies led to 141 of the studied species (~28%) to have no wing loading nor aspect ratio data in the final data set.

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230   When provided, data quality also varied with only 14 of 147 studies providing complete individual

231   level data; however, of those studies only two provided the data as an available supplement. Most

232   studies (71.4%) reported species-level mean and a measure of dispersion (either standard deviation

233   or standard error), and a smaller portion only reporting a mean (9.5%).

234   ## 3.2 Influence of field measurement method on area

235   From the available data, 47 species had records for lift surface area using both tracing and

236   photographs allowing for direct comparison. The models converged, showing caterpillar-like trace

237   plots, and all R-hat values approximated 1. Posterior predictive checks indicated that predicted and

238   observed data had similar distributions, and reflected adequate model fit. However, Pareto shape

239   k parameters indicated the presence of outliers with high influence for both models (Supp. File

240   S2). Measuring lift surface area using a tracing compared to photographs did not show any effect

241   on area estimate (Table 1; Supp. File S2).

242   **Table 1** Bayesian regression outputs for the model comparing between measuring lift surface area

243   using a tracing or a photograph.

Model structure	*Estimate*	Est.Error	L95% CI	U95% CI	Rhat	*Bulk ESS*	*Tail ESS*
Group-Level Effects:							
sd(Reference ID)	0.09	0.03	0.04	0.16	1	4602	7051
sd(Scientific Name)	0.49	0.05	0.40	0.61	1	2803	6403
Population-Level Effects:							
Intercept	4.96	0.08	4.80	5.12	1	1960	4458
method MeasurementTrace	0.01	0.06	-0.09	0.13	1	7001	10561
					Bayes R^2	94.99%	

244

245   From the collected wing morphology data, only 6 species (*Cynopterus sphinx*, *Cynopterus*

246   *brachyotis*, *Cynopterus horsefieldii*, *Molossus molossus*, and *Pteropus tonganus*) had records

247   using both definitions of area. The primary difference between lift surface area and wing area is

248   the inclusion of the uropatagium in LSA and from the available species only *Molossus molossus*

249   has a relatively large uropatagium. As such, while modeling was not possible to determine the

250   differences between using wing area or lift surface area on wing loading and aspect ratio, we did

251   see a difference in wing loading (LSA definition mean wing loading = 19.7 Nm^{-2}; wing area

252   definition mean wing loading = 16.5) and aspect ratio (LSA aspect ratio = 7.7; wing area aspect

253   ratio = 8.7) estimates for *Molossus molossus*. The observed pattern is consistent theoretically

254   considering that as the tail area increases in relation to the size of the wing area both aspect ratio

255   and wing loading will decrease as they are inversely proportional to area.

256   3.3 Global species data availability

257   After removing outlier records and correcting for methodology we compiled a dataset comprised

258   of 430 species with at least some available wing morphology data (wingspan, wing area, wing

259   loading, relative wing loading or aspect ratio), representing approximately 27.8 % of global bat

260   species. When data was available, trait completeness was high as 311 of the 430 species had

261   estimates for all relevant traits (mass, wingspan, wing area, aspect ratio, wing loading, and relative

262   wing loading). However, overall wing morphology data showed low trait coverage across most

263   bat families, with only 7 families showing ≥ 50% data availability and only one of those families

264   (Mormoopidae) consisted of more than 6 species (Figure 3). For genus level trait coverage, 79

265   genera (36.1%) had no species with available data. Within families that had at least one species

266   with available data, the percent of genera without any data ranged from 22.6% to 66.7% (Suppl

267   Table S1). Primarily, species wing loading data were derived from one or two studies (78.7%),

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268   while only 23 species had five or more references. Aspect ratio showed a similar pattern with only

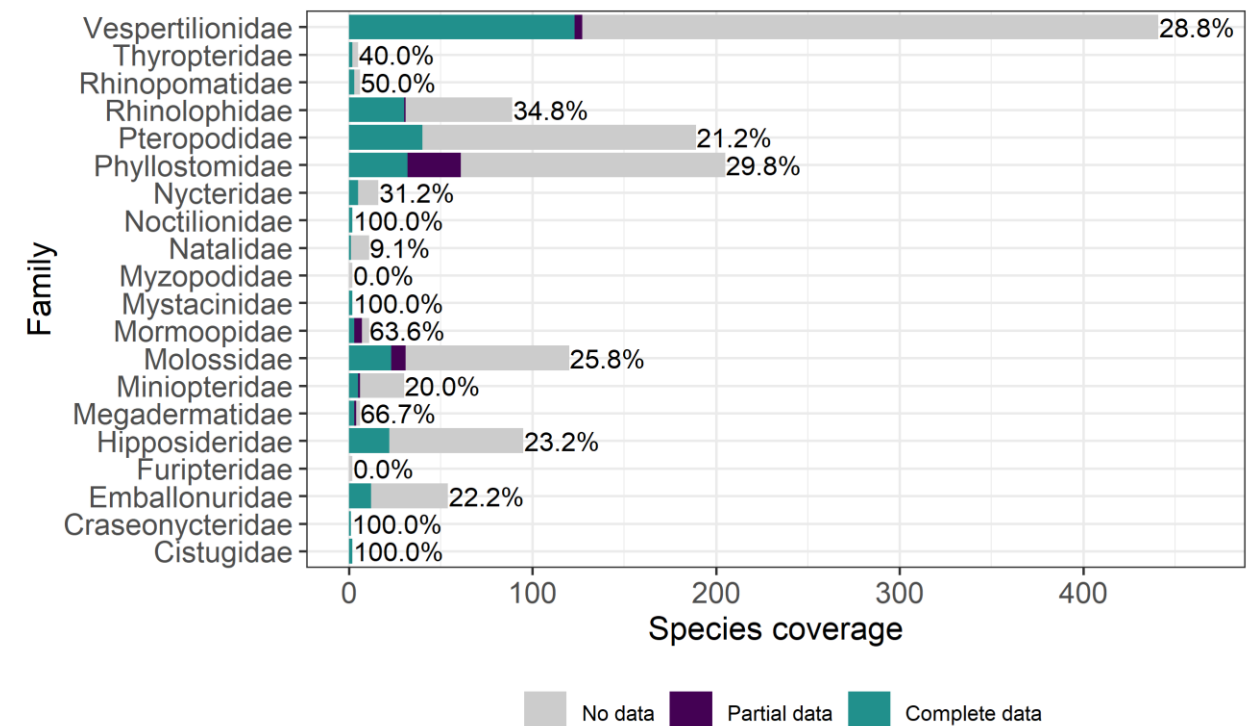269   25 species with five or more references.

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272   **Figure 3** Wing morphology data availability for bat species by family, showing species with no

273   data (e.g. without wing loading and aspect ratio), partial data (wing loading and aspect ratio but

274   not mass, wingspan, and/or lift surface area) or complete data (all relevant trait data available)

275   along with the percent of species within each family that have at least some data available.

276   Across all IUCN categories wing morphology data exhibited a high volume of missingness (Figure

277   4). The distribution of available data follows a similar pattern to overall species categorization.

278   Only 17 of the 193 species listed in a Threatened category (Vulnerable, Endangered, Critically

279   Endangered), have wing morphology data and all 17 had full trait completeness (i.e. available data

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280   for mass, wingspan, wing area, wing loading, relative wing loading, and aspect ratio). When

281   looking at listed threats under the IUCN assessment for threatened species, we saw similar patterns

282   of low trait coverage across threat categories. Additionally, all the threats identified as high impact

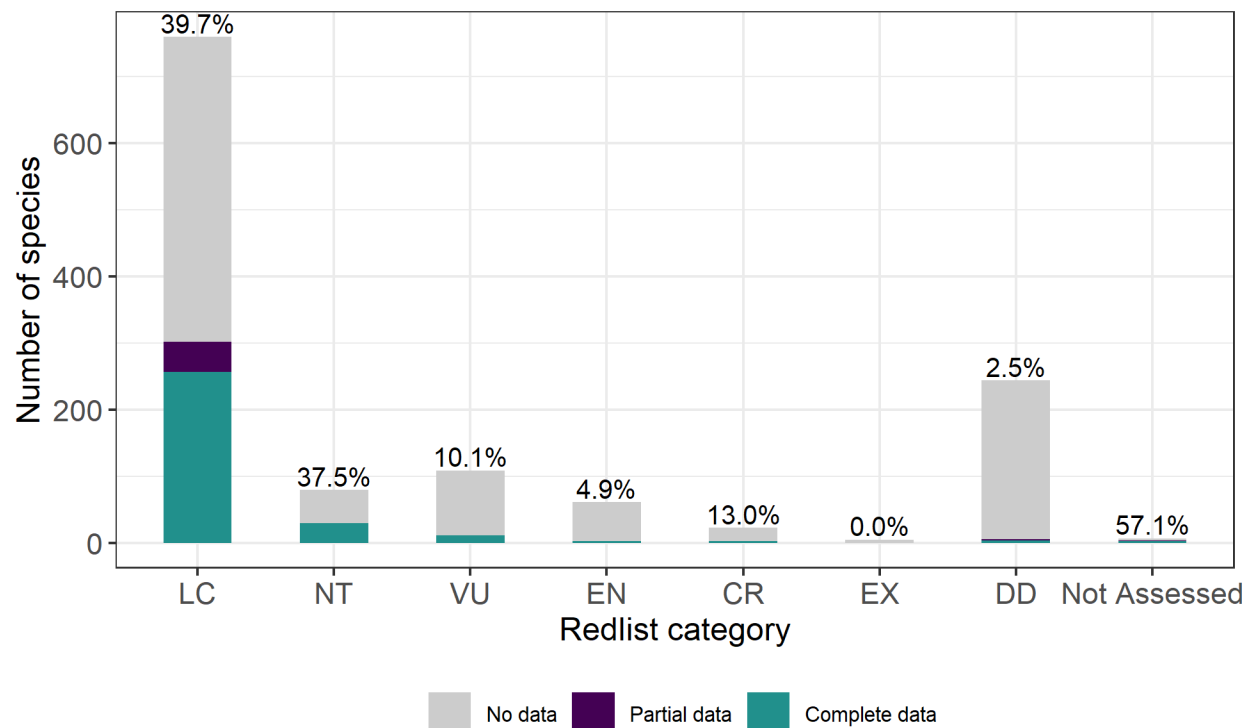283   from the IUCN assessment had no wing morphology data available (Supp. Table S2).

284

285   **Figure 4** Bat wing morphology data availability (species with both wing loading and aspect ratio)

286   for IUCN Redlist category Least Concern (LC), Near Threatened (NT), Vulnerable (VU),

287   Endangered (EN), Critically Endangered (CR), Extinct (EX), Data Deficient (DD), and species

288   not currently assessed by the IUCN. Percentages above the bars indicates percent of species with

289   at least some available trait data for each category.

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291   Trait coverage for wing loading and aspect ratio varied between ecoregions but was typically low

292   overall (Supplemental Table S3). Only the Nearctic realm exhibited trait coverage over 50% with

293   an ecoregion wide trait coverage of 65.5% for both wing morphology and aspect ratio. The

294   Nearctic also exhibited the highest median assemblage-level trait coverage for both wing loading

295   and aspect ratio, followed by the Palearctic and Indomalayan realms; however, several realms

296   showed high variation in assemblage-level trait coverage (Figure 5b). Trait coverage varied within

297   the geopolitical regions we defined for the Palearctic, with the Asiatic Palearctic exhibiting lower

298   median trait coverage than the other regions (Figure 5c). The global wing morphology dataset

299   showed geographic biases with North America and Europe having higher overall trait coverage

300   for species, while Asiatic Palearctic, tropical Australasia, and tropical Africa had relatively lower

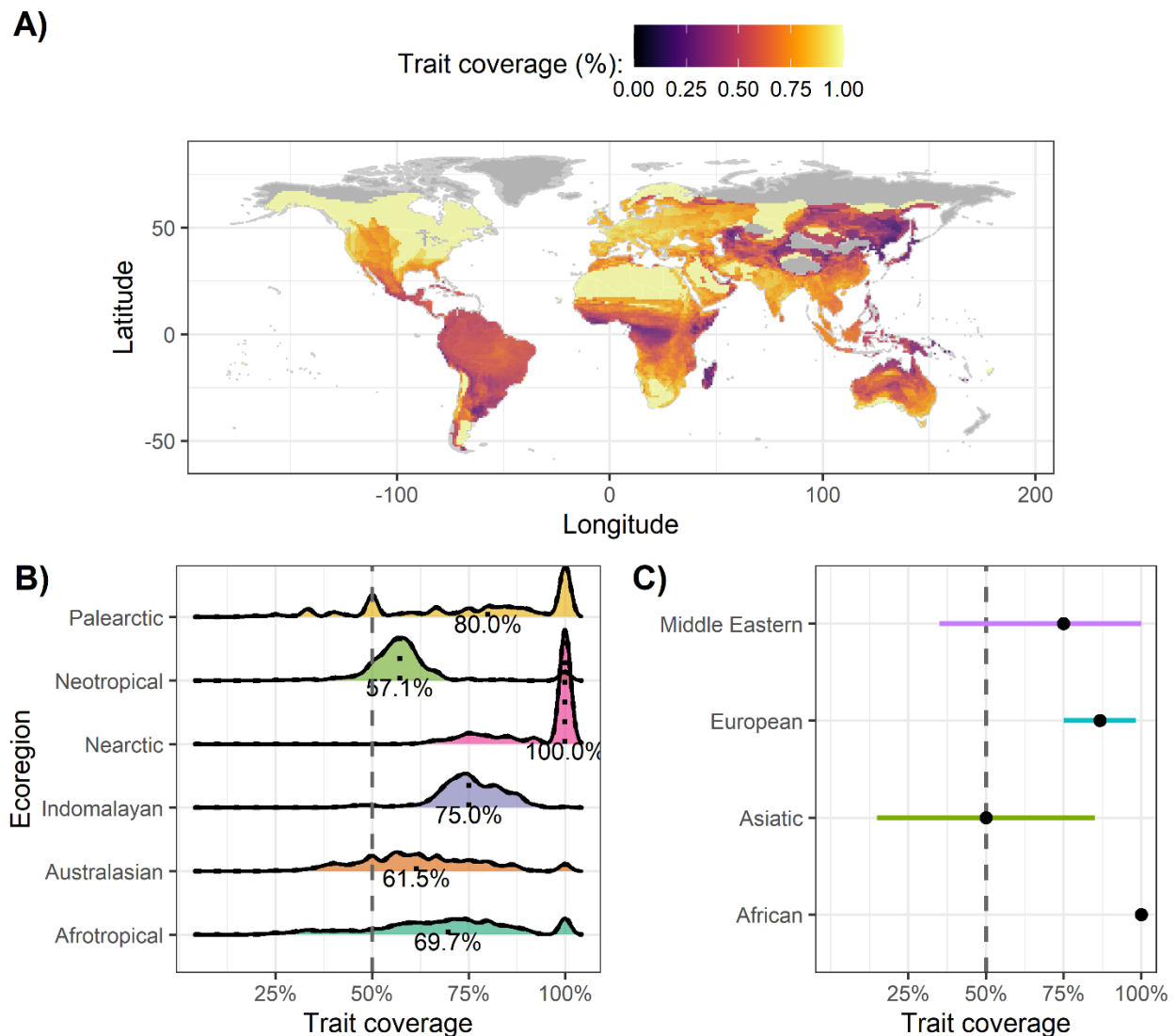301   data coverage.

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Figure 5 (A) Global assemblage-level wing loading trait coverage. Darker colors highlight regions with relatively fewer number of species with available data. Light grey indicates that either no bat species are present or that range data was not available. (B) Assemblage-level wing loading trait coverage density for each with the median coverage value. (C) Median and interquartile range of wing loading trait coverage for geopolitical regions within the Palearctic ecoregion.

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4. Discussion

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310   Overall, bat wing morphology data exhibits poor trait coverage, with a small proportion ($< 30\%$)

311   of species with available data for each trait we assessed. We identified several underlying issues

312   within the wing morphology literature that inhibit consolidating a global database. From the

313   available data, bat wing morphology trait coverage showed both taxonomic and geographic biases

314   which limits assessing conservation status and threat risks globally with the currently available

315   data.

316   While we found variation in field techniques for measuring wing area, most studies adopted one

317   of two methods which produced similar area estimates. One of the biggest issues arose from

318   semantic ambiguity in terminology, primarily wing area definition, and this should be addressed.

319   We suggest following Schneider et al., (2019) and adopting an Ecological Trait-data Standard

320   Vocabulary (ETS), which as a minimum requires studies to report a value (column named

321   *traitValue*), standard units for the value (*traitUnit*), a unified descriptive name (*traitName*), and a

322   scientific taxon (*scientificName*). Using the standard column naming is not required but facilitates

323   faster inclusion into a unified database. Trait name is important for maintaining consistency across

324   studies, and for bat wing morphology we propose a set of unambiguous trait names (Table 2;

325   Figure 6).

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327 **Table 2** Proposed unified terminology for bat wing morphology traits, with the current potentially ambiguous terms the suggested
328 unified trait name, the suggested trait unit, and an unambiguous definition for the proposed trait

| Current terms	unified traitName	traitUnit	Description
Wingspan	wingspan	cm	The linear distance from wing tip to wing tip or measured as the distance from the midline of the body to a single wing tip doubled
Wing area; Lifting surface area	wing_area	cm2	The full area of the patagium, directly measured from a wing tracing or photograph
	lifting_surface_area	cm2	The total area of the patagium, uropatagium (if present), and body excluding the head
	wing_area_rec	cm2	The rectangular approximation of the patagium based on the wing length (measured from the edge of the body to the wing tip) multipiled by the wing wing width (measured starting at the fifth digit down to the tip of the fifth digit)
Aspect ratio	partial_aspect_ratio	NA	The wingspan squared divided by wing_area
	total_aspect_ratio	NA	The wingspan squared divided by lifting_surface_area
Wing loading	partial_wing_loading	Nm^{-2}	mass x gravitational constant divided by wing_area
	total_wing_loading	Nm^{-2}	mass x gravitational constant divided by lifting_surface_area
Relative wing loading; geometric wing loading	relative_partial_loading	NA	partial_wing_loading divided by mass raised to 1/3. Note that mass and not weight (mass * g) should be used
	relative_total_loading	NA	total_wing_loading divided by mass raised to 1/3. Note that mass and not weight (mass * g) should be used

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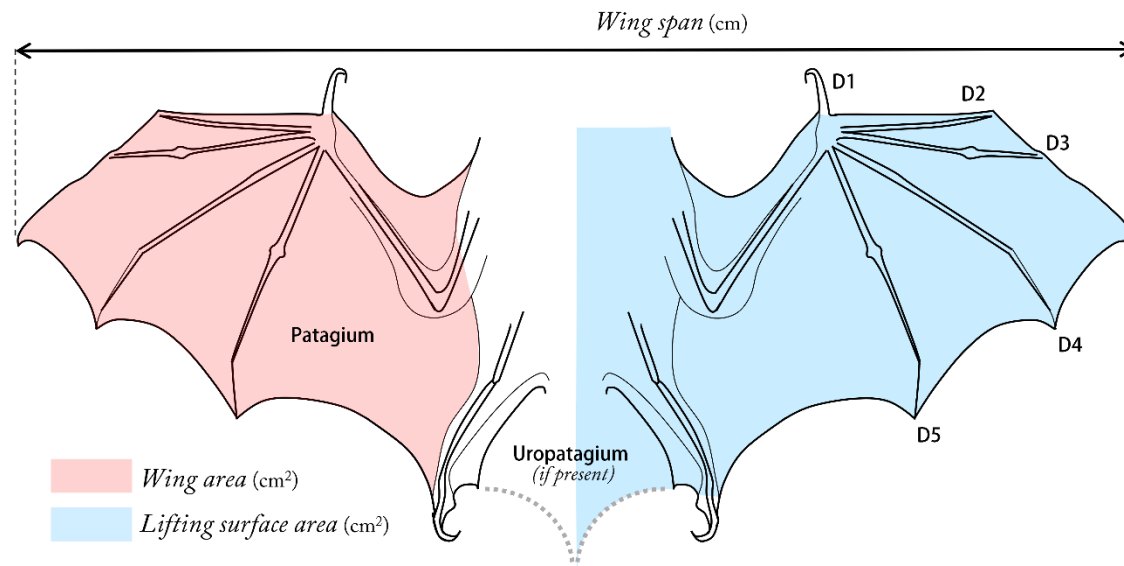
Figure 6 Bat wing outline designating regions included in the "wing area" definition (left) and lifting surface area (right).

We also identified numerous gaps in data reporting across studies. We documented that primary morphological traits such as forearm, mass, wingspan, and wing area were underreported in the literature. Additionally, few studies (14) provided fully open available individual level data, and more problematically several studies (13) either provided no data, did not provide species level data, or only presented data in a figure. Open Science can facilitate the development and accelerate the growth of trait datasets (Gallagher et al 2020), thus we suggest that studies collecting bat wing morphology traits should adopt an Open Science approach to address the data reporting gap. Omitting trait values limits the ability to unify trait data and estimate additional variables. For instance, we saw that not reporting mass along with either wing loading or relative wing loading meant that we were not able to generate an estimate for both traits. Additionally, while we focused on wing loading and aspect ratio, several other methods exist for comparing bat wing morphology such as geometric analysis (Dietz, Dietz & Siemers, 2006; Schmieder et al., 2015), and indices

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345   based on skeletal measures (Findley, Studier & Wilson, 1972; Bader et al., 2015). Providing values

346   for all relevant traits measured in a study, can help either estimate or even calculate other trait

347   values strengthening the overall data availability.

348   Wing morphology data are not available for most bat species across multiple families and regions.

349   Geographically, several regions showed low data availability particularly South America,

350   Madagascar, parts of Oceania, the Middle East, and Asiatic Palearctic. The geographic biases raise

351   several concerns with applying a global approach to meta-analysis using wing morphology data.

352   Bat populations face a myriad of threats which vary depending on the region (Frick, Kingston &

353   Flanders, 2020). We found a similar trend in low trait coverage for threatened species (González-

354   Suárez, Lucas & Revilla, 2012). We identified gaps in data coverage for IUCN threatened category

355   species, as well as when considering trait coverage for specific high impact threats. Given the

356   underlying low trait coverage and biases, it is critical for researchers using bat wing morphology

357   to consider the missingness mechanism within their framework (Nakagawa & Freckleton, 2008;

358   Baraldi & Enders, 2010). For instance, missing data patterns within conservation status and

359   specific threats could confound results and inhibit conservation-based conclusions

360   Missing data pattens (e.g. whether data is missing at random or not) within available trait data,

361   also relates to how ecologists should handle missing data cases (Nakagawa & Freckleton, 2008).

362   Missing data rarely occurs completely at random, which means that simple approaches such as

363   case deletion can introduce strong biases (Nakagawa & Freckleton, 2008; González-Suárez, Lucas

364   & Revilla, 2012; Pakeman, 2014). As missing data is ubiquitous across fields, multiple new

365   techniques have been developed to impute non-random missing data (Bruggeman, Heringa, &

366   Brandt, 2009; Pantanowitz & Marwala, 2009; van Buuren & Groothuis-Oudshoorn, 2010). A

367   major concern with applying any imputation with is the volume of missing data relative to

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368   available data. Penone et al. (2014) showed that some techniques could handle up to 40% missing

369   data when traits were phylogenetically conserved. In addition to accounting for phylogeny,

370   relationships between traits can be used in imputation models. Incorporating additional traits to

371   impute bat wing morphology data may provide a promising approach, as other traits are globally

372   well sampled for mammals; however, it unclear whether this is the case specifically for bats (Etard

373   et al., 2020). Globally trait coverage for bat wing morphology does not meet the 40% criteria, but

374   studies focused on a smaller subset could still benefit from data imputation.

Caveats

376   We did not conduct our literature review searches in additional languages, which may change the

377   data availability coverage especially in regions where English is not the primary language. Some

378   of the geographic biases we observed may be a factor of limiting our search language to English.

379   English is not the primary language in several of the regions with low trait coverage. However,

380   our English search provides a large starting centralized dataset and additionally provides a

381   framework for adding bat wing morphology data from non-English sources and from grey

382   literature. Additionally, the English search did return three papers in Chinese. We advocate for

383   using the data presented in this study only as a starting point for developing a more robust global

384   repository for bat wing morphology. As the global database grows it will be important to revisit

385   our assessment of taxonomic and geographic biases. To this end we have provided R code to easily

386   facilitate future reevaluations, as well as a bat wing morphology database with three levels:

387   individual level data, study level data, and pooled species level data.

388

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